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On the Classification of the Early Tertiary Erinaceomorpha (Insectivora, Mammalia)

MICHAEL J. NOVACEK,[1] THOMAS M. BOWN,[2]
AND DAVID SCHANKLER[3]

ABSTRACT

Definitions are provided for three Early Tertiary families of Erinaceomorpha. The family Dormaaliidae includes *Dormaalius, Macrocranion, Scenopagus, Ankylodon, Crypholestes, Sespedectes,* and *Proterixoides*. Several of these genera are traditionally known collectively as "Adapisoricidae," but *Adapisorex* is probably an erinaceid and the name Adapisoricidae is therefore unavailable for the above listed taxa. Dormaaliids are characterized by a reduction in size and complexity of the anterior premolars, a reduced, premolariform P_4, and several other dental specializations. A second family, the Amphilemuridae includes *Amphilemur, Gesneropithex, Alsaticopithecus,* and *Pholidocercus*. Amphilemurids have inflated, bunodont cheek teeth that superficially resemble primate dentitions. A third family, the Erinaceidae, includes the Early Tertiary genera *Litolestes, Leipsanolestes, Entomolestes, Neomatronella, Eolestes, Adapisorex, Cedrocherus,* and living and fossil members of the Galericinae, Brachyericinae, and Erinaceinae. Another member of the Erinaceidae is *Dartonius,* proposed here as a new designation for "*Leptacodon*" *jepseni*. Several erinaceomorphs are either too generalized in structure, too divergent, or too poorly represented to allow assignment to any of the above families. These *incertae sedis* taxa are *Diacodon, Adunator* (including *Mckennatherium*), *Diacocherus, Litocherus, Talpavus,* and *Talpavoides*.

INTRODUCTION

The erinaceomorph insectivores are a critical group for understanding eutherian phylogeny. Erinaceomorphs have been variously cited as ancestors or close relatives of tupaiids, primates, bats, dermopterans, and several other major eutherian taxa. The classification of Erinaceomorpha has, however, been subject to diverse interpretations. Gregory (1910, p. 464) named the Section Erinaceomorpha as a group including Erinaceidae, Leptictidae, and Dimylidae (table 1). Simpson (1945) retained these families and

[1] Chairman and Assistant Curator, Department of Vertebrate Paleontology, American Museum of Natural History.
[2] Geologist, U.S. Geological Survey, Denver, Colorado 80225.
[3] Research Assistant, Department of Geological and Geophysical Sciences, Princeton University, Princeton, New Jersey 08544.

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TABLE 1
Classifications of Erinaceomorph Insectivorans

Gregory, 1910
- Order Insectivora
  - Suborder Lipotyphla
    - Section Zalambdodonta (incl. Families Centetidae, Potamogalidae, Solenodontidae, Necrolestidae, Chrysochloridae)
    - Section unnamed (incl. Family Pantolestidae)
    - Section Erinaceomorpha (incl. Families Leptictidae, Erinaceidae, Dimylidae)
    - Section Soricomorpha (incl. Families Soricidae, Talpidae)
  - Suborder Unnamed (incl. Family Hyopsodontidae)

Simpson, 1945
- Order Insectivora
  - Superfamily Deltatheridioidea
  - Superfamily Tenrecoidea
  - Superfamily Chrysochloroidea
  - Superfamily Macroscelidoidea
  - Superfamily Soricoidea
  - Superfamily Pantolestoidea
  - Superfamily Mixodectoidea
  - Superfamily Erinaceoidea
    - Family Zalambdalestidae
    - Family Dimylidae
    - Family Leptictidae (incl. *Gypsonictops, Prodiacodon, Acmeodon, Emperodon, Myrmecoboides, Adapisorex, Diacodon, Parictops, Protictops, Ictops, Leptictis, ?Xenacodon, ?Sespedectes*)
    - Family Erinaceidae
      - Subfamily Echinosoricinae (incl. *Entomolestes, Proterioxoides, Metacodon, Ankylodon, Proterix, Brachyerix, Metechinus, Meterix, Neurogymnurus, Lantanotherium, Galerix, Pseudogalerix, Echinosorex, Hyolomys, Podogymnura, Neotetracus*)
      - Subfamily Erinaceinae (incl. *Tetracus, Palaeoerinaceus, Tupaiodon, Palaeoscaptor, Parvericius, Aethechinus, Erinaceus, Atelerix, Hemiechinus, Paraechinus*)

Van Valen, 1967
- Suborder Erinaceota
  - Superfamily Erinaceoidea
    - Family Adapisoricidae
      - Subfamily Geolabidinae
      - Subfamily Adapisoricinae (incl. *Mckennatherium, Leptacodon, Adunator, Adapisorex, Paschatherium, Messelina*)
      - Subfamily Creotarsinae (incl. *Litolestes, Xenacodon, Talpavus, Creotarsus, Dormaalius, Entomolestes, Scenopagus, Macrocranion, Amphilemur, Sespedectes, Proterixoides, Amphidozotherium, Ictopidium, Tupaiodon*)
      - Subfamily Nyctitheriinae
    - Family Erinaceidae
      - Subfamily Galericinae
      - Subfamily Erinaceinae
    - Family Talpidae
  - Superfamily Soricoidea

Russell, Louis, and Savage, 1975
- Suborder Erinaceomorpha
  - Family Adapisoricidae
    - Subfamily Adapisoricinae (incl. *Adapisorex*)
    - Subfamily Dormaaliinae (incl. *Litolestes, Leipsanolestes, Dormaalius, Entomolestes, Neomatronella, "Leptacodon" jepseni, Macrocranion, Scenopagus, ?Proterixoides, ?Sespedectes, Talpavus, Ankylodon*)

Krishtalka, 1976a
- Family Adapisoricidae (incl. *Mckennatherium, Scenopagus, Ankylodon, Macrocranion, Talpavus*)
- Family Erinaceidae (incl. *Litolestes, Leipsanolestes, ?Entomolestes* [*grangeri*], and the subfamilies Galericinae and Erinaceinae)

THIS PAPER:
- Suborder Erinaceomorpha
  - Family Dormaaliidae (incl. *Dormaalius, Macrocranion, Scenopagus, Ankylodon, Crypholestes, Sespedectes, Proterixoides*)
  - Family Amphilemuridae (incl. *Amphilemur, Gesneropithex, Alsaticopithecus, Pholidocercus*)
  - Family Erinaceidae (incl. *Litolestes, Leipsanolestes, Adapisorex, Entomolestes, Neomatronella, Eolestes, Cedrocherus, Dartonius, Proterix,* and subfamilies Galericinae, Erinaceinae, and Brachyericinae)
  - Erinaceomorpha, *incertae sedis* (incl. *Diacodon, Adunator* [incl. *Mckennatherium*], *Diacocherus, Litocherus, Talpavus, Talpavoides*)

added Zalambdalestidae in his Superfamily Erinaceoidea. Saban (1954), frequently and incorrectly cited as the author of the Erinaceomorpha, expanded this category with his inclusion of the pantolestids, apheliscids, zalambdalestids, and macroscelidids, in addition to the families recognized by Gregory. Several authors in more recent years (Butler, 1956a, 1972; McDowell, 1958; McKenna, 1960, 1975; Russell, 1964; Van Valen, 1967;

Novacek, 1973, 1976, 1977; Russell, Louis, and Savage, 1975; Krishtalka, 1976) have argued that Erinaceomorpha seems realistically limited to the Erinaceidae and other early taxa generally recognized as "adapisoricids." Several matters remain unresolved. Sigé (1977) regards nyctitheriids as members of the Erinaceomorpha *contra* opinions of McKenna (1975), Krishtalka (1976a, 1976b), Novacek (1976), Bown and Schankler (1982), and others. There is also argument as to whether dimylids (see Schmidt-Kittler, 1973) belong to the Erinaceomorpha (following Van Valen, 1967; Butler, 1972; Novacek, 1976) or the Soricomorpha (following Schmidt-Kittler, 1973; McKenna, 1975). "Amphilemurids" (Heller, 1935) were transferred from Erinaceomorpha to Primates by Russell, Louis, and Savage (1975) but were returned to Erinaceomorpha by Koenigswald and Storch (1983). Gingerich (1983) has united several problematic "adapisoricids" as members of the new subfamily Litocherinae. Here we address problems of relationships among the selected members of the Erinaceomorpha; namely, the Early Tertiary taxa commonly recognized as erinaceids, adapisoricids, and amphilemurids. Our purpose is to provide a consensus statement on the higher level taxonomy of the Erinaceomorpha that reflects, with some modification, our independent studies of this problem (e.g., Bown and Schankler, 1982; Novacek, 1982).

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ABBREVIATIONS

AMNH, American Museum of Natural History
HTM, Institut Royal des Sciences Naturelles de Belgique
UCMP, University of California Museum of Paleontology, Berkeley
USGS, United States Geological Survey
YPM, Yale Peabody Museum

SYSTEMATICS

CLASS MAMMALIA LINNAEUS, 1758

ORDER INSECTIVORA CUVIER, 1817

SUBORDER ERINACEOMORPHA GREGORY, 1910

DIAGNOSIS: Insectivorans with the following combination of dental features that distinguish them from other early eutherian clades. P_1 small, single-rooted and P_{2-3} dominated by a single cusp. P_4 with a short, basined or unbasined talonid; P_4 talonid cusps absent, or, if present, diminutive. M_{1-3} paraconids compressed, lophid-like, or cristiform. Molar trigonid cusps lower, less sectorial, and more anteriorly canted than in *Kennalestes, Cimolestes, Procerberus, Asioryctes,* palaeoryctids (*sensu stricto*), primitive leptictids (e.g., *Prodiacodon*), geolabidids, early miacids, and creodonts. Talonids on M_{1-2} nearly as wide or wider than trigonids. M_{1-3} with high entoconids and low hypoconids often flattened in early stages of wear. P^3 small, triangular in occlusal outline (secondarily enlarged in some taxa). P^4 hypocone usually present, metacone weak or absent, metastylar crest strong. M^{1-2} semirectangular with narrow stylar shelves, distinct hypocones, and posterolingual cingula.

INCLUDED FAMILIES: Dormaaliidae Quinet, 1964; Erinaceidae Fischer de Waldheim, 1817; ?Dimylidae Schlosser, 1887; Amphilemuridae Heller, 1935.

DISCUSSION: The above characterization of the Erinaceomorpha is discussed at length by Novacek (1982). Polarity assessments of tooth characters in early insectivorans are difficult, owing to the often subtle differences observed among these taxa. Only the combination of the above cited features serves to distinguish erinaceomorphs; no single feature is by itself diagnostic. Readers familiar with the problem will be aware of other early eutherians that share at least some of these traits (see also Novacek, 1982). Nevertheless, the diagnosis is useful if it is assumed that high-cusped, sectorial molars and premolars seen in early leptictids, palaeoryctids, and a variety of Cretaceous eutherians represent a

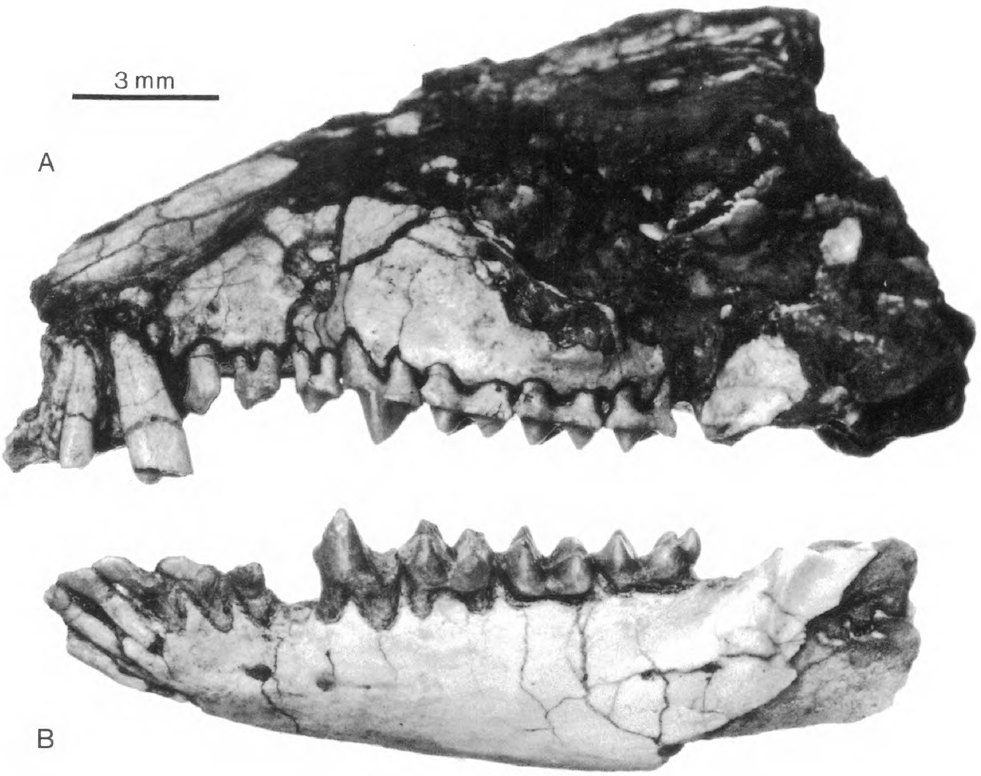

FIG. 1. *Macrocranion nitens*, partial cranium and jaws (USGS 3676). A, lateral view of left premaxilla, maxilla, I^{2-3}, C, P^{1-4}, M^{1-3} (P^1 is a reversed photograph of P^1 from right maxilla); B, lateral view of left ramus with root of I_1, I_2, I_3, C, P_1, P_2, P_4 (P_3 damaged), M_{1-3}. Note small, procumbent, and single-rooted P_{1-2}. Specimen from Willwood Formation (lower Eocene), Bighorn Basin, Wyoming.

closer approximation of the primitive eutherian morphotype.

FAMILY DORMAALIIDAE QUINET, 1964

Figures 1–3

DIAGNOSIS (as modified from Russell, Louis, and Savage, 1975; Krishtalka, 1976a, 1977; Novacek, 1982): Shares with erinaceids the following derived erinaceomorph characters: P^4 metacone lost or greatly reduced.* Hypocone on P^4 present.* Talonid on M_1 as wide or wider than trigonids. Small hypoconulid on M_{1-2}. Lower trigonid relief on M_{1-3}. M_3 reduced. Differs from primitive erinaceids in having the following derived features: P_4 with notably short talonid (P_4 talonid somewhat more elongate in *Scenopagus hewettensis*). P_{2-3} reduced, P_2 single-rooted. Anterior lower premolars generally reduced and procumbent. Paraconid on M_{1-3} transversely oriented and crestiform; trigonids anteroposteriorly compressed in occlusal view. M_{1-3} trigonids less erect, more canted, than in early erinaceids. (* indicates characters for teeth not known in all dormaaliids.)

INCLUDED TAXA:

Dormaalius Quinet, 1964. early Eocene, Europe.
- *Dormaalius vandebroeki* Quinet, 1964.

Macrocranion Weitzel, 1949. early–middle Eocene, Europe and North America.
- *Macrocranion tupaiodon* Weitzel, 1949.
- *Macrocranion tenerum* (Tobien, 1962), Russell, Louis, and Savage, 1975.
- *Macrocranion nitens* (Matthew, 1918) Krishtalka, 1976a.

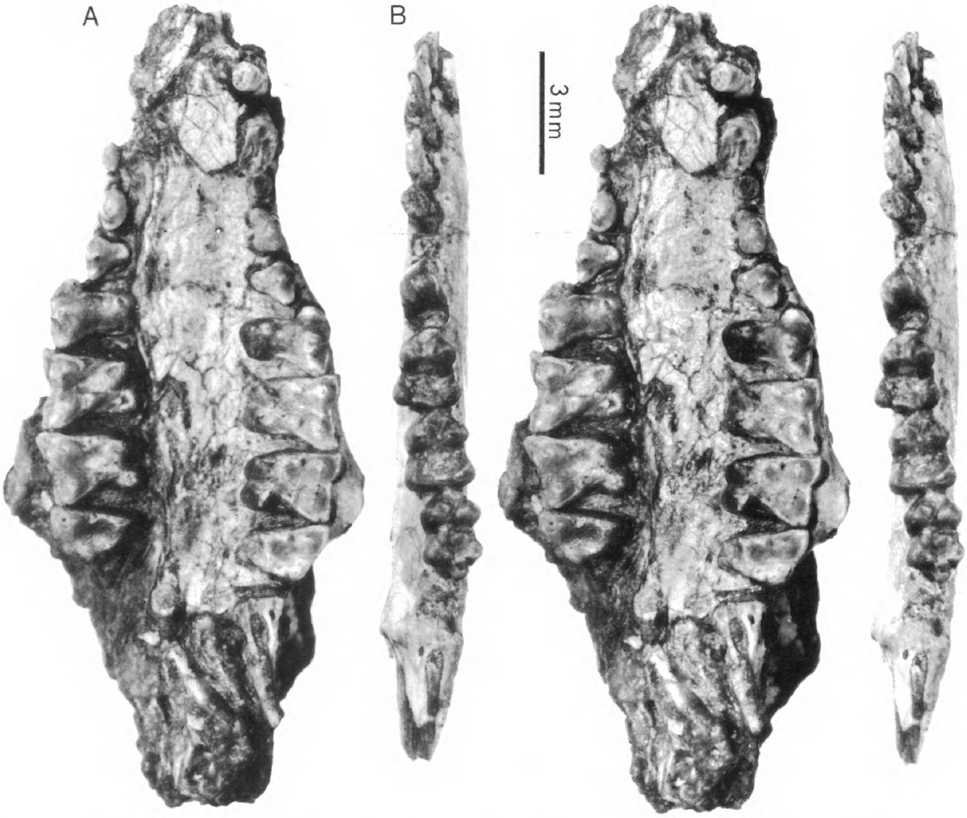

FIG. 2. *Macrocranion nitens,* partial cranium and jaws (USGS 3676). Stereophotographs of A, ventral view of palate and upper dentition (right and left I^1, right I^{2-3}, and left P^1 missing); B, occlusal view of left ramus with I_{1-2}; C, P_{1-4}, M_{1-3}. Note lack of metacone on P^4, well-developed hypocones on M^{1-2}, short heel on P_4, and crestiform paraconid on M_{1-3} (see diagnosis for Dormaaliidae).

Macrocranion robinsoni Krishtalka and Setoguchi, 1977.
Macrocranion sp. (in Russell, Louis, and Savage, 1975).
"?*Entomolestes* cf. *nitens*" (in Russell, Louis, and Savage, 1975).
Scenopagus McKenna and Simpson, 1959. early–middle Eocene, North America.
Scenopagus mcgrewi McKenna and Simpson, 1959.
Scenopagus edenensis (McGrew, 1959), Robinson in McKenna, Robinson, and Taylor, 1962.
Scenopagus priscus (Marsh, 1872), Krishtalka, 1976a.
Scenopagus hewettensis Bown and Schankler, 1982.
Ankylodon Patterson and McGrew, 1937. middle Eocene–early Oligocene, North America.
Ankylodon annectens Patterson and McGrew, 1937.
Ankylodon progressus Galbreath, 1953.
Crypholestes (Novacek, 1976), Novacek, 1980. middle Eocene, North America.
Crypholestes vaughni (Novacek, 1976), Novacek, 1980.
Sespedectes Stock, 1935. middle Eocene, North America.
Sespedectes singularis Stock, 1935.
Proterixoides Stock, 1935. middle Eocene, North America.
Proterixoides davisi Stock, 1935.
"Erinaceid-like genus and species" (UCMP 101420, see Novacek, 1976), middle Eocene, North America.

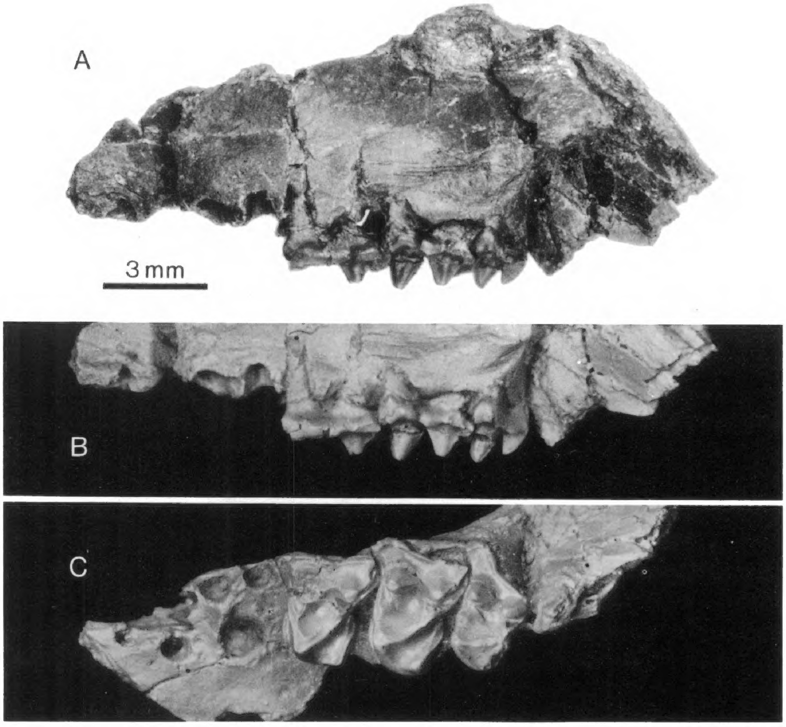

FIG. 3. *Macrocranion* sp., left maxillary fragment with M^{1-3} (alveoli for P^{3-4}) (AMNH 46897). Lateral view of A, original; B, epoxy cast; C, occlusal view of cast. Specimen from Quarry 88, Arroyo Blanco, San Jose Formation (lower Eocene), San Juan Basin, New Mexico. See also Maier (1979).

DISCUSSION: The majority of taxa included within the Dormaaliidae are perhaps more familiar to specialists as adapisoricids. However, we believe that the Adapisoricidae is an inappropriate designation for any erinaceomorph higher taxon. As noted below, *Adapisorex* seems excluded from a group comprising most of the forms usually called adapisoricids; thus the name Adapisoricidae is unavailable for this group. Genera currently recognized as "adapisoricids" can be linked with more modern erinaceids by several derived characteristics (see Russell, Louis, and Savage, 1975; Krishtalka, 1976a, 1977; Novacek, 1976, 1982). These features are also commonly used to recognize "adapisoricids," but this family cannot be distinguished as a monophyletic group by application of the same features suggesting monophyly for the Erinaceomorpha. Krishtalka (1977) has attempted to remedy this situation by suggesting three derived dental traits of "adapisoricids" (within which he included "*Mckennatherium*" [see remarks below], *Scenopagus, Macrocranion, Dormaalius, Talpavus* and, tentatively, *Sespedectes* and *Proterixoides*) that differentiated this group from erinaceids. These were: (1) lophid-like transverse paraconids on M_{1-3}; (2) M_1 with relatively broader talonid than trigonid and M_2 with relatively narrower talonids than trigonids; and (3) high entoconids and low, flat hypoconids.

Use of these characters for the purpose of defining "adapisoricids" is, however, problematic. There is notable variation within "adapisoricids" *sensu* Krishtalka (1977) in the structure of the paraconid (Bown and Schankler, 1982; Novacek, 1982). Moreover, *Entomolestes grangeri*—recognized as an erinaceid by Krishtalka (1976a)—has a lingually positioned, crestiform paraconid similar to that in the putative "adapisoricids" "*Mckennatherium*" *ladae* and *Macrocranion nitens*.

Variation is also seen in other allegedly diagnostic features of "adapisoricids." "*Mckennatherium*" *ladae* differs from the typical adapisoricid condition in having a narrower talonid than trigonid on M_1 (M_1 trigonids and talonids are of subequal widths in *Talpavus nitidus*). Erinaceids supposedly differ from "adapisoricids" in having a relatively wider M_2 talonid, but this condition is also known in the "adapisoricid" *Macrocranion nitens* (see table 4 in Krishtalka, 1976a). Finally, the "adapisoricid" entoconid/hypoconid relationship suggested as diagnostic by Krishtalka (1976a, 1977) also occurs in the putative erinaceid *Entomolestes grangeri.*

Even if one could arrive at an internally consistent definition of the Adapisoricidae, the name of the group is an unfortunate choice. The type genus *Adapisorex,* represented by *A. gaudryi* Lemoine 1883, is markedly different from other "adapisoricids" (see Clemens, 1973; Russell, Louis, and Savage, 1975). Krishtalka (1976a, 1977) suggested that *Adapisorex* is an erinaceid. Russell, Louis, and Savage (1975) separated *Adapisorex* as the sole member of the Adapisoricinae and applied Dormaaliinae (originally established by Quinet, 1964, as a monotypic family) as the subfamily-group name for all other "adapisoricids." Bown and Schankler (1982) argued that *Adapisorex* is an "erinaceid-like" condylarth, similar to *Phenacodaptes* or *Apheliscus* (Gazin, 1959). There is a striking similarity, however, between *Adapisorex* and erinaceids and reference to that family seems justified (see comments below).

Similar problems involve *Creotarsus.* This genus serves as the type of the Creotarsinae, a subfamily recognized by Van Valen (1967) to be "adapisoricid" and to include many of the genera considered here. *Creotarsus,* represented solely by the type specimen, has some rather strong hyopsodontid-like characters in the lower premolars and molars, and we do not recognize the Creotarsinae as a valid erinaceomorph group.

If *Adapisorex* and *Creotarsus* do not belong in the group generally termed Adapisoricidae, a group of early non-erinaceid erinaceomorphs requires diagnosis and an appropriate name. Bown and Schankler (1982) argued that clearer definition is attained by excluding some of the more primitive erinaceomorphs from the group, including "*Mckennatherium*" *ladae* (and its probable close relatives *Adunator* and "*Diacodon*" *minutus,* see Bown and Schankler, 1982, and discussion below) and thus recognizing a group of more limited diversity. These authors raised the rank of the Dormaaliinae (of Russell, Louis, and Savage~~, 1975~~) for such a purpose, but this action, without re-diagnosis, is not satisfactory. The published definition for dormaaliines (see Russell, Louis, and Savage, 1975, p. 134) does not exclude more primitive erinaceomorphs nor does it aptly describe all *sensu stricto* dormaaliids. For example, the diagnosis given by Russell, Louis, and Savage (1975) states that the talonids are generally wider than the trigonids in the lower molars of dormaaliids, but this does not account for the variation in lower molar proportions in erinaceids and other erinaceomorphs.

To complicate matters, *Dormaalius* is a problematic type genus for a higher taxon. Quinet (1964) erected this name for two species, *D. vandebroeki* and *D. simonsi,* but did not provide differential diagnosis of either species, and did not explicitly establish a type species for the genus or type specimen for either species. All these actions violate sufficiently the *International Code of Zoological Nomenclature* (Stoll et al., eds., revised 1964; articles 13, 67, 72) to constitute grounds for suppression of the generic and specific names. Finally, as Bown and Schankler (1982) observe, *Dormaalius* is poorly represented and the meager available material suggests very close similarity to *Macrocranion.*

Some of these problems have been resolved by recent work. Russell, Louis, and Savage (1975) clarify most of the ambiguities of Quinet's (1964) original designation of *Dormaalius.* The type specimen of *D. vandebroeki* is validly designated as HTM (Institut Royal des Sciences Naturelles de Belgique) 66, a lower jaw with P_4 and alveoli for other teeth. *Dormaalius vandebroeki* was originally referred by Teilhard de Chardin (1927) to his *Omomys belgicus.* The type mandible (HTM 66) was subsequently figured by Quinet (1964) and given the name *D. vandebroeki.* Russell, Louis, and Savage (1975) argue convincingly that *D. simonsi* is a junior synonym of *D. vandebroeki. Dor-*

maalius is clearly distinct from the type species of *Macrocranion* (*M. tupaiodon*) in having a relatively larger P_4 compared to M_1.

For these reasons, Novacek (1982) endorsed Bown and Schankler's (1982) recognition of the family Dormaaliidae. This action does not solve all the problems with *Dormaalius*. As Krishtalka (1977) noted, *Dormaalius* is very similar to *Macrocranion nitens* (figs. 1–3) and several other species referred to this genus (see above listing). Moreover, *Dormaalius* is so poorly represented that its generic distinction from *Macrocranion* (as currently defined) is open to question. *Dormaalius* differs, however, from *M. nitens* in being significantly smaller and in having a relatively anteroposteriorly shorter, less labially expanded P_4 talonid; a small, shallow basin lingual to the crest connecting the talonid cusp to the posterior wall of the trigonid of P_4; a less transverse, labially expanded M_2 talonid with a weak hypoconulid represented by a slight rise on the crest joining the hypoconid and entoconid (M_2 hypoconulid is distinct and somewhat "swollen" in *Macrocranion nitens*). These differences are slight but adequate for separating *Dormaalius* from the member of *Macrocranion* it most resembles. Moreover, as is stated in article 40 of the *International Code*, 1964, the recognition of *Dormaalius* as a junior synonym of *Macrocranion* would not justify the rejection of the family-group name Dormaaliidae. In the interest of consistency, we retain the Dormaaliidae to designate the group including *Dormaalius, Macrocranion,* and several other genera listed above.

Macrocranion was allocated to the Amphilemuridae of Heller (1935; see also McKenna, 1960) by Tobien (1962), although Van Valen (1967) recognized the genus as a member of the Creotarsinae. It is now evident, based on excellent new skeletal material, that amphilemurids are referable to the Erinaceomorpha, but separable from erinaceids and *Macrocranion* and other "adapisoricid" or "dormaaliid" genera considered here (Koenigswald and Storch, 1983; and comments below).

Because the matter is not discussed elsewhere, we briefly mention our reasons for excluding *Ictopidium* from the Dormaaliidae. *Ictopidium* is represented by a single species, *I. lechei* Zdansky (1930) from the Eocene of China. Zdansky misinterpreted the structure of P_4 in this species as "molariform," and he accordingly assigned *Ictopidium* to the Leptictidae. The genus was transferred to the Erinaceidae by Butler (1956b), and subsequently to the Creotarsinae by Van Valen (1967). *Ictopidium* shows the reduced P_4 talonid characteristic of dormaaliids. However, the genus is poorly represented by its holotype, a partial lower jaw fragment with P_{3-4}, M_2 and the trigonid of M_3. Reference to the Erinaceidae as suggested by Butler (1956b) seems doubtful because the alveolar space occupied by M_1 does not suggest that this tooth was any larger than M_2. Hence, the progressive reduction in size of M_1 through M_3 that is diagnostic of erinaceids is not apparent in *Ictopidium*. P_3, P_4 morphology of *Ictopidium* is also unlike the typical condition in other erinaceomorphs. These teeth have high, piercing trigonid cusps more reminiscent of palaeoryctoids. Moreover, the hypoconulid of M_2 is very small and placed lingually and adjacent to the entoconid, a condition that contrasts strongly with that in erinaceomorphs. *Ictopidium* is Insectivora *incertae sedis* with possible affinities to palaeoryctids or soricomorphs.

Ankylodon represents perhaps the most controversial allocation within the Dormaaliidae. Fox (1983) claimed recently that, contrary to widespread opinion (Butler, 1972; Krishtalka, 1976a; Lillegraven, McKenna, and Krishtalka, 1981; Novacek, 1982), this genus is a soricomorph rather than an erinaceomorph. His evidence (*ibid.*) for this claim includes the presence in *Ankylodon* of (1) an enlarged I^1; (2) a raised anterior and ventral rim of the orbit; (3) anteriorly elongated palatines; (4) the opening of the lacrimal duct within the orbit; (5) a reduced (incomplete?) zygomatic arch; and (6) inferred origin of snout muscles on the maxillary root of the zygomatic arch. Of these, only character 1 seems to support Fox's argument. Character 2 (cf. a diversity of mammals, including tupaiids, macroscelidids, dermopterans, and some erinaceids—but note lack in most tenrecids) and character 3 (cf. leptictids, macroscelidids) are widely distributed and

possibly primitive eutherian traits. Character 4 may be derived for Eutheria but it is also present in leptictids, dermopterans, macroscelidids, and, notably, in some galericine erinaceids. Character 5 is ambiguous because the material Fox described is damaged in the zygomatic region. Moreover, the zygomatic is slender in certain erinaceids (cf. *Hyolomys, Neotetracus*). It is the marked reduction or loss of the jugal elements, not simply the narrow zygomatic arch, that is a significant characteristic of soricomorphs. Character 6 is subject to considerable variation in insectivorans (as noted by Fox, 1983), and the arrangement of the snout muscles and their attachments in the fossil *Ankylodon* are open to various interpretations. This problematical evidence hardly challenges the association of *Ankylodon* with erinaceomorphs based on shared-derived features of the dentition (Butler, 1972; Krishtalka, 1976a; Novacek, 1982; and McKenna and Lillegraven, in prep.). We thus retain *Ankylodon* within Erinaceomorpha and, more specifically, we ally this genus with *Scenopagus* and an unnamed dormaaliid from the middle Eocene of San Diego (UCMP 101420, see Novacek, 1976, 1982).

No attempt is made here to provide a classification of higher resolution for the Dormaaliidae. Novacek (1982) has suggested a possible cladistic pattern of relationships for some of the taxa listed here. Any formalization of this scheme first requires more detailed published comparisons of *Sespedectes* and *Proterixoides* with "amphilemurids" and other erinaceomorphs. The tortuous history of allocations for dormaaliids and related forms is summarized in table 1.

FAMILY AMPHILEMURIDAE HELLER, 1935

DIAGNOSIS (from Koenigswald and Storch, 1983): $\frac{3}{3}\ \frac{1}{1}\ \frac{4}{4}\ \frac{3}{3}$ and fully functional milk teeth. Relatively little differentiation between antemolar teeth. P_{1-3} single-rooted, crowded, and progressively procumbent anteriorly. Marked size difference between P^4_4 and P^3_3. C_1 small, premolariform, or incisiform. I_{1-3} relatively small, spatulate. P_4 premolariform with unicuspid talonid and distinct crista obliqua and talonid basin. Molars bunodont with low, inflated crowns. Reduction in size from M^1_1 to M^3_3. Upper molars with mesostyle, very narrow stylar shelves, low metacrista, well-developed paraconules and metaconules. M^{1-2} somewhat quadrate in occlusal outline with strong hypocones. Lower molars with transverse lophid-like paraconid, and showing only slight difference in height between trigonid and talonid. Hypoconid as high or higher than entoconid. Talonid wider than trigonid. M_{1-2} semirectangular in outline (for expanded diagnosis that includes general erinaceomorph characters, see Koenigswald and Storch, 1983, p. 451).

INCLUDED TAXA:

Amphilemur Heller, 1935. middle Eocene, Europe.
 Amphilemur eocaenicus Heller, 1935.
Gesneropithex Hürzeler, 1946. late Eocene, Europe.
 Gesneropithex peyeri Hürzeler, 1946.
Alsaticopithecus Hürzeler, 1947. middle Eocene, Europe.
 Alsaticopithecus leemanni Hürzeler, 1947.
Pholidocercus Koenigswald and Storch, 1983. middle Eocene, Europe.
 Pholidocercus hassiacus Koenigswald and Storch, 1983.

DISCUSSION: Amphilemurids are clearly more allied with erinaceomorphs (McKenna, 1960; Koenigswald and Storch, 1983) than with primates (Russell, Louis, and Savage, 1975). This group, however, shows traits that suggest a number of alternative relationships within Erinaceomorpha. The quadrate outline of the molars, the well-developed hypocones, and the slight progressive reduction in size from M_{1-3} suggest affinity with erinaceids. The bunodont crown patterns of the molars are reminiscent of features in the dormaaliids *Sespedectes, Proterixoides,* and *Crypholestes.* The reduction and procumbent form of P_{1-3} strongly resemble conditions in *Macrocranion.* Detailed dental comparisons with some, but not all, of the relevant taxa led Koenigswald and Storch (1983, p. 477) to conclude that amphilemurids were not closely related to the groups they recognized as Adapisoricidae (essentially equivalent to the Dormaaliidae of this paper) and Erinaceidae. The above comparisons suggest,

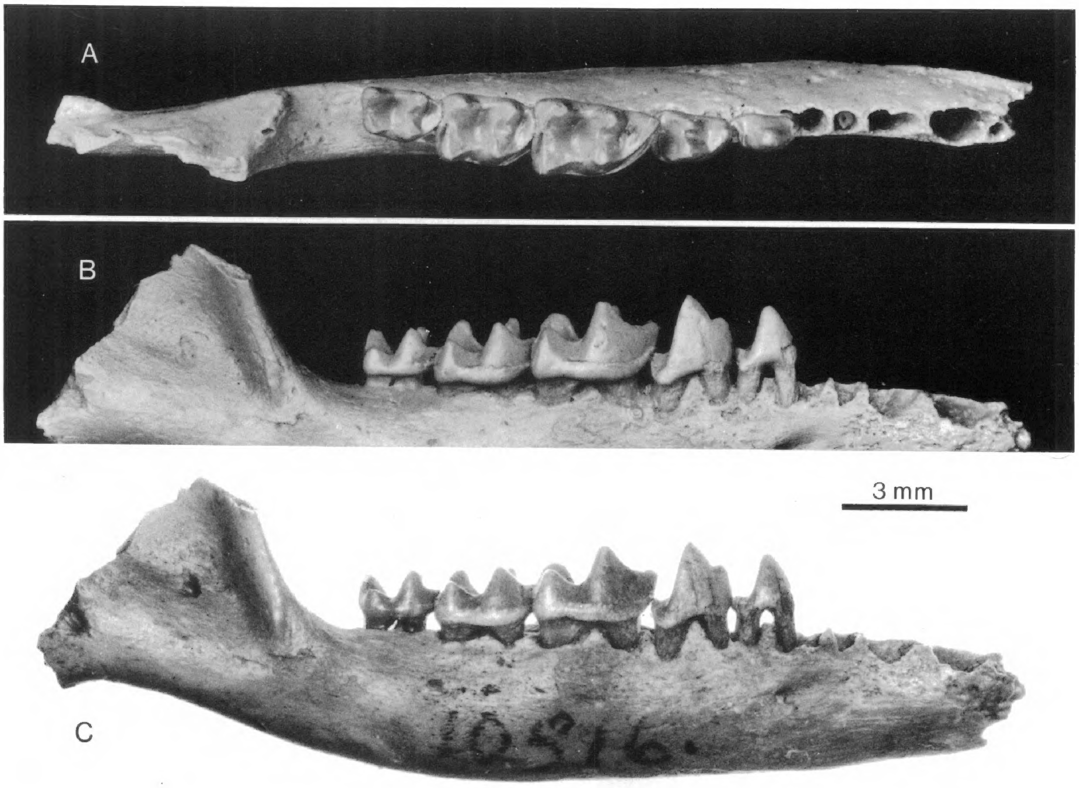

FIG. 4. *Galerix socialis,* right ramus with P_3, P_4, M_{1-3} and alveoli for I_3, C, P_{1-2} (AMNH 10516D). A, occlusal; B, lateral views of epoxy cast; C, lateral view of original. Note projecting prevallid shearing surface on M_1, reduction in size from M_1 to M_3 (see diagnosis for Erinaceidae). Specimen from La Grive (Miocene), St. Albans, Isère, France.

nonetheless, the potential for documentation of a close relationship between amphilemurids and some other erinaceomorph subgroup. Pending such a study, the Amphilemuridae are recognized here as a separate family of erinaceomorph insectivorans.

FAMILY ERINACEIDAE (FISCHER DE WALDHEIM), 1817

Figures 4–10

DIAGNOSIS (after Krishtalka, 1976a, 1977; Butler, 1948): Erinaceids share the following defining features: Lower molars show progressive reduction in size from M_1 to M_3. Lower molars semirectangular in occlusal view, with some degree of exodaenodonty (i.e., bases of labial trigonid and talonid cusps are swollen). Talonid basin formed as a V-shaped valley by flat internal walls of hypoconid and entoconid. M_1 paraconid salient and anteriorly projecting, elongating prevallid shearing wall. Hypoconulids on M_{1-2} markedly reduced and positioned at or just lingual to midline of the crown on posterior wall. M^{1-2} (where known) are semirectangular or quadrate in outline. Hypocones are better developed on M^{1-2} than in dormaaliids. M^3 is markedly reduced and usually oval in outline. In most erinaceids, hypocones are connected via a crest to postprotocrista.

INCLUDED TAXA: The following species are recognized as Erinaceidae but are excluded from the subfamilies Galericinae, Brachyericinae, Erinaceinae, and Protericinae:

Litolestes Jepsen, 1930. late Paleocene, North America.

FIG. 5. *Galerix socialis,* left ramus with P_1 (damaged), P_{2-4}, M_{1-2}, and alveoli for I_{1-3}, C, M_3 (AMNH 10499). A, occlusal; B, lateral views of epoxy cast; C, lateral view of original. For locality information see figure 4.

Litolestes ignotus Jepsen, 1930 (but excluding *L. notissimus* and *L. lacunatus,* seem comments in Krishtalka, 1976a, pp. 29–30; Gingerich, 1983).

Leipsanolestes Simpson, 1928. late Paleocene, early Eocene, North America.

Leipsanolestes siegfriedti Simpson, 1928.

Entomolestes Matthew, 1909. middle Eocene, North America.

Entomolestes grangeri Matthew, 1909.

Neomatronella Russell, Louis, and Savage, 1975. early Eocene, Europe. (Described as *Matronella* in Russell, Louis, and Savage, 1975; see note, p. 177, *op. cit.*)

Neomatronella luciannae Russell, Louis, and Savage, 1975.

Eolestes (Bown, 1979), Bown and Schankler, 1982. early Eocene, North America.

Eolestes simpsoni (Bown, 1979), Bown and Schankler, 1982.

Dartonius, new genus. early Eocene, North America.

Dartonius jepseni (McKenna, 1960), new species.

Adapisorex Lemoine, 1883. middle–late Paleocene, Europe.

Adapisorex gaudryi Lemoine, 1883.

Adapisorex abundans Russell, 1964.

Cedrocherus Gingerich, 1983. late Paleocene, North America.

Cedrocherus ryani Gingerich, 1983.

The following species are provisionally referred to the Galericinae:

Erinaceid sp. from type specimen of Tepee Trail Formation (AMNH 88288), middle Eocene, North America (in McKenna and Krishtalka, in prep.; Krishtalka, 1976a).

Erinaceid sp. in Krishtalka and Setoguchi, 1977. middle Eocene, North America.

For taxa referred to the erinaceid subfamilies Brachyericinae, Protericinae, Galericinae, and Erinaceinae, see Butler (1948), Van

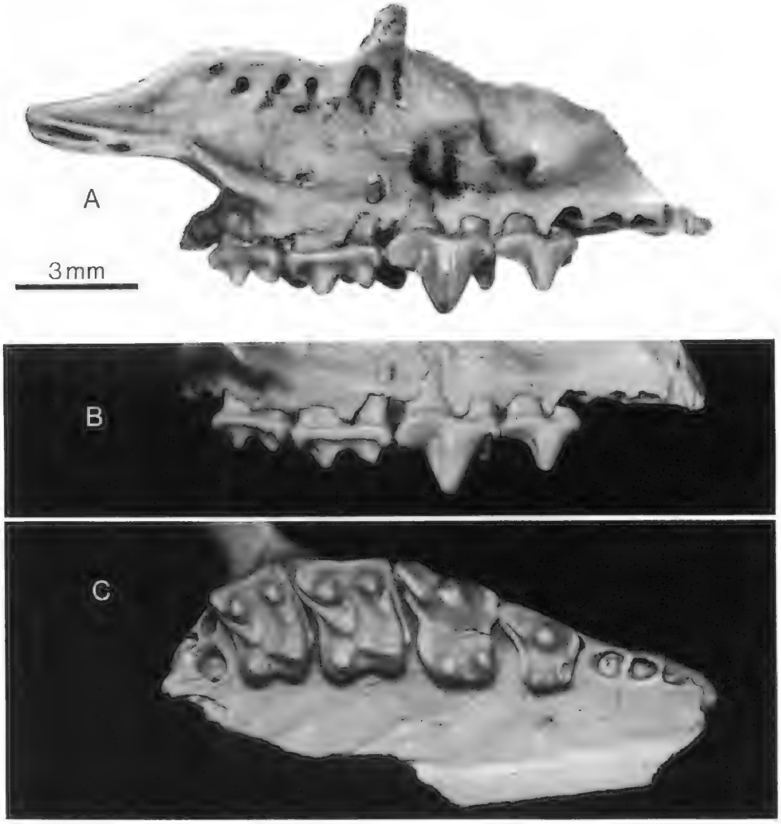

FIG. 6. *Galerix socialis,* maxillary fragment with P^{3-4}, M^{1-2}, and alveoli for P^2, P^3, M^3 (AMNH 10499). A, lateral view of original; B, lateral; C, occlusal views of epoxy cast. For locality information see figure 4.

Valen (1967), Rich and Rich (1971), and Rich (1981).

DISCUSSION: The above diagnosis for the Erinaceidae is limited to dental characters, as pre-Oligocene erinaceids are virtually unknown from other parts of the skeleton. It should be noted, however, that known skulls of both fossil and Recent erinaceids show a suite of distinctive characteristics (Butler, 1948; Rich, 1981).

There are four recognized erinaceid subfamilies—the Galericinae (figs. 4–6) (equals the Echinosoricinae of earlier papers), the Erinaceinae, the Protericinae, and the Brachyericinae—but we do not assign any of the named Paleocene or Eocene erinaceids to these groups. Contrary to statements by Krishtalka (1976a, 1977), we do not see a clear galericine-erinaceine split exemplified by the dental variation in these early taxa (see Novacek, 1982). Moreover, assignment of these species is difficult because the most primitive erinaceid subfamily, the Galericinae, is poorly defined, as this group is recognized primarily by the lack of erinaceine dental specializations. A reasonable approach to the problem is to look once again at the evidence for monophyly of the Galericinae represented by living taxa and more completely preserved fossils.

Krishtalka (1976) clarified considerably the position of certain Early Tertiary erinaceomorphs that shared derived dental features with established erinaceids. *Litolestes* (*ignotus*) (fig. 7), *Leipsanolestes* (figs. 8, 9), and *Entomolestes* (fig. 10) all show the progressive reduction of M_{1-3}, and the more quadrate dimensions of the lower molars noted in

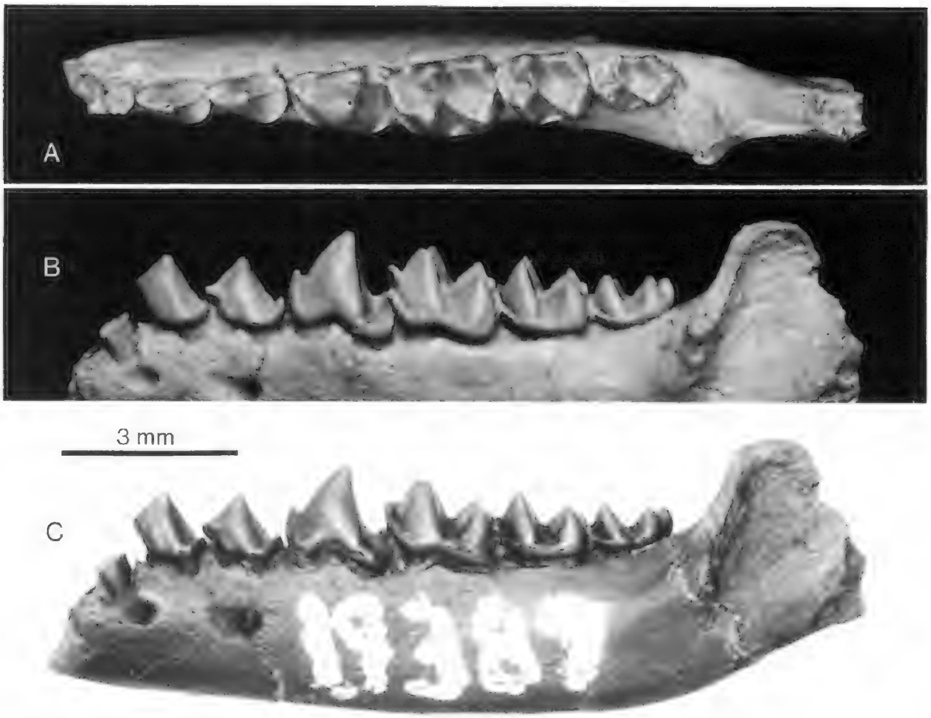

FIG. 7. *Litolestes ignotus*, left ramus with P_{2-4}, M_{1-3} and root of P_1 (PU 19387). A, occlusal; B, lateral views of epoxy cast; C, lateral view of original. Note progressive reduction in size from M_1 to M_3. Specimen from Schaff Quarry southwest, Upper Polecat Bench Formation (upper Paleocene), Park County, Wyoming.

the above diagnosis. *Leipsanolestes* differs from more specialized erinaceids and from dormaaliids in having an elongate P_4 with a well-developed talonid (fig. 9), a primitive erinaceomorph trait (Novacek, 1982). The shortening of the talonid of P_4 was thus developed independently in erinaceids and dormaaliids.

As noted above, *Adapisorex* is a likely member of the Erinaceidae (*fide* Krishtalka, 1976a, p. 7; Koenigswald and Storch, 1983). This genus has the quadrate upper molars with well-developed hypocones, the marked reduction in size of M_3 relative to M_2 and the reduced oval-shaped M^3 characteristic of erinaceids. Other features indicate a more conservative morphology. P^4 in *Adapisorex* has a small, but distinct, metacone, the P^4 hypocone is either weak or absent, and, as in *Leipsanolestes*, P_4 talonid is well developed, with one or more cusps and a shallow basin. P_4 in the type of *Adapisorex abundans* shows strong molariform development, but the tooth may be a deciduous premolar (see Russell, 1964 for description).

Cedrocherus, a monotypic genus from the late Paleocene of northwestern Wyoming, was described by Gingerich (1983) as a member of his proposed adapisoricid subfamily Litocherinae. Here we regard *Cedrocherus* as closely related to, and possibly synonymous with, *Litolestes*. Although Gingerich (1983) included *Litolestes* and *Leipsanolestes* along with *Cedrocherus* in the Litocherinae, these taxa in their erinaceid specializations differ distinctly from other "litocherines" (see comments below). *Cedrocherus* was distinguished by the shape of the entoconid on M_1 and M_2 and the very marked gradient in decreasing size from M_{1-3} (Gingerich, *ibid.*, p.

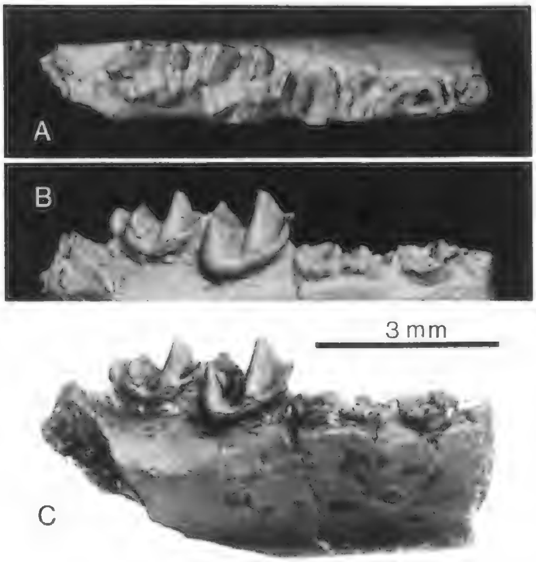

FIG. 8. *Leipsanolestes siegfriedti,* right mandible fragment with M_{2-3} and roots of P_4, M_1 (AMNH 22157, Type). A, occlusal; B, lateral views of epoxy cast; C, lateral view of original. Note reduced M_3. Specimen from Bear Creek, Fort Union Formation (Clarkforkian, upper Paleocene–lower Eocene), Carbon County, Montana.

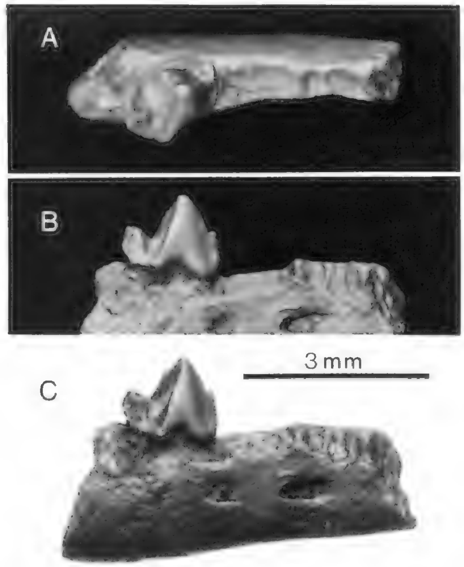

FIG. 9. *Leipsanolestes siegfriedti,* right mandible fragment with P_4 and alveoli for P_2, P_3 (AMNH 22231). Posterior fragment of ramus not shown. A, occlusal; B, lateral views of epoxy cast; C, lateral view of original. Note distinct talonid basin and talonid cusps. For locality information see figure 8.

237). It is debatable whether these characters justify recognition of a new genus, rather than simply a new species of *Litolestes. Cedrocherus* is presently only represented by a single species (*C. ryani*) and a single jaw fragment with M_{1-3}. Additional material is required to substantiate its generic status.

Of these early Tertiary erinaceids the assignment of *Entomolestes* seems the most problematic. This genus shows a mosaic of erinaceid and dormaaliid traits (fig. 10). Like the latter, *Entomolestes* has a P_4 with a very short talonid, strong crestiform paraconid on M_{1-3}, reduced, somewhat procumbent, P_2, P_3 (described as P_3, P_4 by Krishtalka and West, 1977), and a hypoconid that is much lower than the entoconid in M_{1-3}. Like erinaceids, *Entomolestes* shows a progressive reduction in dimension of M_1 to M_3 (although this reduction is not so marked in M_2 as in other erinaceids), and the labial margins of the lower molar cusps are expanded, giving the crowns a more quadrate outline in occlusal view. *Entomolestes* also has a two-rooted P_2 (Krishtalka and West, 1977, fig. 2), whereas known P_2s of dormaaliids are single-rooted. This condition in *Entomolestes* is simply primitive; some early Galericines (e.g., *Litolestes, Galerix, Neurogymnura*) have two-rooted P_2s (fig. 5) but in most erinaceids this tooth is single-rooted. Loss of roots and size reduction of anterior premolars seems subject to much convergence among early Tertiary insectivorans.

In light of these comparisons, we retain *Entomolestes* within erinaceids. We also concur with Krishtalka's (1976a, 1977) recognition of *Leipsanolestes, Litolestes,* and *Neomatronella* as early erinaceids. To this list we add *Eolestes simpsoni,* described by Bown and Schankler (1982), and an early Eocene form described as "*Leptacodon*" *jepseni* by McKenna (1960). A new designation and comparative diagnosis for "*L.*" *jepseni* follow.

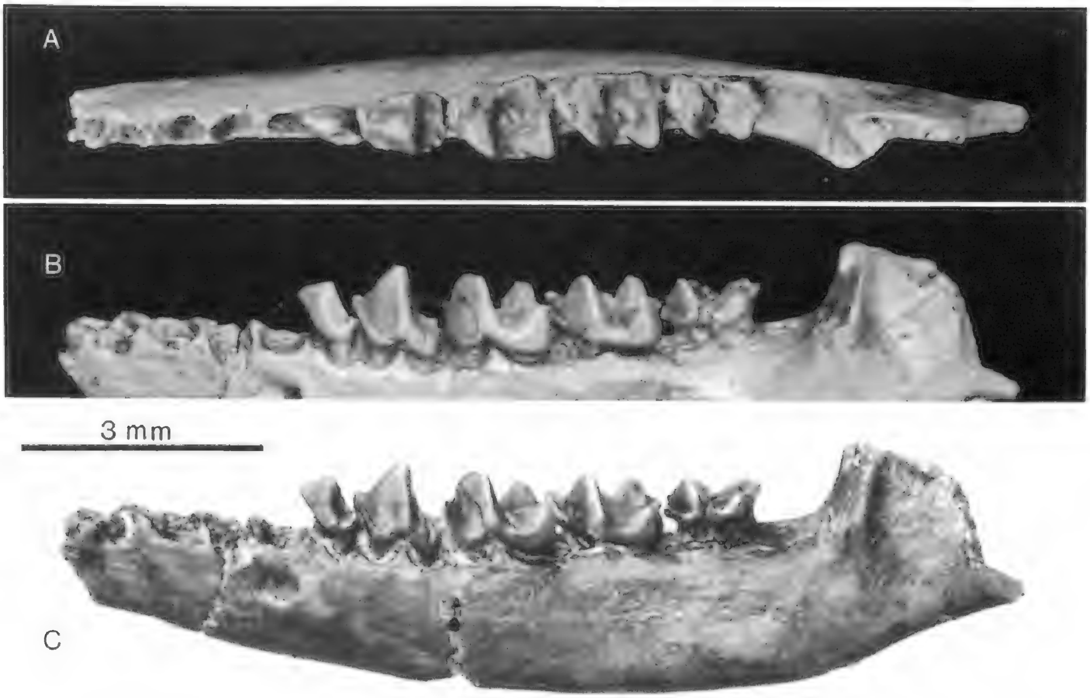

FIG. 10. *Entomolestes grangeri*, left ramus with P_3, P_4, M_{1-3} and alveoli for C, P_1, P_2 (AMNH 11485, Type). A, occlusal; B, lateral views of epoxy cast; C, lateral view of original. Specimen from Grizzly Buttes West, Bridger B, Bridger Formation (middle Eocene), Bridger Basin, Wyoming.

DARTONIUS, NEW GENUS

TYPE AND ONLY SPECIES: *Dartonius jepseni* (McKenna, 1960, p. 51).

DIAGNOSIS: Erinaceid genus that differs from *Entomolestes grangeri* in smaller size, in having a smaller P_3/P_4 ratio, in having a shorter, more curved prevallid, in having less exodaenodont labial margins of the molars, and in having smaller and less linguolabially compressed molar entocristids. From the approximately coeval erinaceid *Eolestes simpsoni*, *Dartonius* differs in having a smaller P_4/M_1 ratio, in having a better developed P_4 talonid basin, in having a shorter, less attenuated entocristid, in lacking a connection of the cristid obliqua with the metaconid, and in having a more acute paracristid notch on the molars. Differs from *Talpavus* and dormaaliids in features that define erinaceids (see comments below).

ETYMOLOGY: For Nelson Horatio Darton, pioneer western North American geologist.

Dartonius jepseni (McKenna, 1960)

Leptacodon jepseni McKenna, 1960, p. 51.

MATERIAL: Holotype UCMP 45949, fragment of right ramus with P_3–M_2 (formerly preserving P_2; McKenna, 1960, fig. 24). UCMP 47023, 47155 (McKenna, 1960, p. 51); YPM 30559 (Bown and Schankler, 1982, fig. 24E); possibly AMNH 56313 (Delson, 1971, p. 328).

OCCURRENCE: early Wasatchian (early Eocene) Wasatch Formation, northwest Colorado and northeast Wyoming, and Willwood Formation (upper *Haplomylus-Ectocion* Range Zone of Schankler, 1980, northwest Wyoming).

DIAGNOSIS: Same as for genus.

DISCUSSION: In 1960, McKenna named *Leptacodon jepseni* for three specimens of a small insectivore from Alheit Pocket in the Four Mile Creek area of northwest Colorado. McKenna rightly believed *Leptacodon* to be

an artificial genus composed of structurally very diverse species, and he considered "*L.*" *jepseni* and "*Leptacodon minutus*" (Jepsen's 1930 *Diacodon minutus*) to be primitive *Entomolestes*-like erinaceoids, perhaps related to the ancestry of Geolabididae (equals Metacodontidae of earlier authors, see Lillegraven, McKenna, and Krishtalka, 1981).

Van Valen (1967) placed *Leptocodon* (including "*L.*" *jepseni*) in the Adapisoricinae, though his construct of that group differs greatly from that of nearly every other author. Delson (1971) referred four new specimens from the early Eocene Powder River local fauna to "*Leptacodon*" *jepseni.* Delson also questioned the generic status of *Leptacodon* and observed that McKenna's "*L.*" *jepseni* is morphologically more similar to the Bridgerian erinaceid *Entomolestes grangeri* Matthew (1909), a view that was advocated by Bown and Schankler (1982) and is endorsed here.

Russell, Louis, and Savage (1975) placed "*L.*" *jepseni* in the Adapisoricidae, but believed that it probably constitutes a new genus closest to *Talpavus* or *Scenopagus.* Those authors discounted the idea of Delson (1971) that "*L.*" *jepseni* shares any close relationship with *Entomolestes.* Krishtalka (1976a, 1977) believed that "*Leptacodon*" *jepseni* was too poorly known to confidently demonstrate its generic status, but agreed with Delson (1971) that the animal probably does not belong in *Leptacodon.* Krishtalka compared "*L.*" *jepseni* with early nyctitheriids and concluded that its affinities probably are closer to the Erinaceomorpha than to the Soricomorpha.

Bown and Schankler (1982) recognized a form close to McKenna's "*Leptacodon*" *jepseni* in collections of fossil lipotyphlan insectivorans from the lower Eocene Willwood Formation of the Bighorn Basin of Wyoming (Yale Peabody Museum 30559). These authors removed three of the four Powder River Basin specimens from "*L.*" *jepseni,* but endorsed Delson's (1971) suggestion that the taxon is very close to the Bridgerian (middle Eocene) erinaceid *Entomolestes grangeri.*

Dartonius (as "*Leptacodon*" *jepseni*) has thus been the source of some confusion since it was first described. Clearly, it differs from the forms with which it has most often been confused (e.g., *Talpavus* and *Scenopagus*; Russell, Louis, and Savage, 1975; and *Leptacodon,* McKenna, 1960; Delson, 1971) by those characters which serve to distinguish the Erinaceidae from the Dormaaliidae and Nyctitheriidae (Soricomorpha), respectively. *Dartonius* in no ambiguous way resembles nyctitheriids (Bown and Schankler, 1982), but could still potentially be confused with *Scenopagus* and *Talpavus* because all are erinaceomorphs.

From *Scenopagus, Dartonius* differs in all its erinaceid features, these including progressive molar size reduction from M_1 through M_3, greater molar exodaenodonty, the flat internal walls of the hypoconulid and entoconid, the anteriorly projecting, salient paraconid of M_1, and the less medial molar hypoconulids. In addition, *Dartonius* shows an anteriorly projecting P_4 paraconid (also distinctive in its close relative *Entomolestes* and erinaceines) that forms a characteristic paraconid notch in labial view. The internal wall of the P_4 paraconid is developed as a flat shelf. The talonid basin of P_4 is relatively broader than in *Scenopagus,* and the entocristid notch is partly filled, forming a sharp mure in labial and lingual views. The molar paraconids and metaconids in *Dartonius* are exactly opposite each other linguolabially, whereas in *Scenopagus* the protoconid is positioned somewhat more posteriorly. *Dartonius* differs from *Talpavus* in its diagnostic erinaceid features, but also in the development of the anteriorly projecting P_4 paraconid, larger molar paraconid, broader P_4 talonid basin, and relatively smaller P_3 with respect to P_4 size. All *Talpavus* and *Scenopagus* species were much larger animals than *Dartonius jepseni.*

We believe that *Dartonius* is closest in morphology (and possibly ancestral, according to T.M.B. and D.S.) to the younger *Entomolestes grangeri.*

ERINACEOMORPHA, *INCERTAE SEDIS*

DISCUSSION: Several Paleocene and Eocene species have been recognized as erinaceomorphs, but their primitive morphology, divergent features, or poor representation preclude their assignment to the Dormaaliidae or the Erinaceidae as defined above. The taxa

here regarded as Erinaceomorpha *incertae sedis* are *Diacodon* (*alticuspis*) Cope (1875), *Talpavus* Marsh (1872), *Talpavoides* Bown and Schankler (1982), *Litocherus* Gingerich (1983), *Adunator* Russell (1964), *Diacocherus* Gingerich (1983) [includes "*Diacodon*" *minutus* of Jepsen (1930)] and *Mckennatherium* Van Valen (1965).

The interrelationships of *Adunator, Mckennatherium,* and "*Diacodon*" *minutus* and the higher level affinities of these taxa are matters of current debate. Krishtalka (1976a) noted that *Adunator* and "*Diacodon*" *minutus* were probably congeneric but distinguished *Mckennatherium* from the former two species on the basis of subtle differences in molar structure. Bown and Schankler (1982) argued that these differences are very slight or virtually unrecognizable and that they do not justify generic separation of the taxa. Following their conclusions, *Mckennatherium* would be recognized as a junior synonym of *Adunator.* This synonymy is of broader interest because *Adunator* has been suggested as showing a strong resemblance to *Haplaletes* and other early hyopsodontid condylarths (Krishtalka, 1976a; Bown and Schankler, 1982). From such considerations, it is clear that only slight departures from the typical erinaceomorph condition can lend a "hyopsodontid appearance" to the lower dentition. A pertinent problem is the lack of an explicit diagnosis of the Hyopsodontidae that accounts for both dentally primitive and dentally derived members of this group. Until such a study is available, *Adunator* and a variety of other species will remain in the limbo between primitive insectivorans and primitive condylarths. Here, we do not exclude the possibility that *Adunator* is a very primitive hyopsodontid, but Novacek recognizes its erinaceomorph affinities to be equally likely. Krishtalka (1976a) has pointed out that although *Adunator lehmanni* shows a swelling of the molar metaconids reminiscent of hyopsodontids, this genus does not approach the low, bulbous, and almost bunodont condition of the molar cusps in *Haplaletes* and other hyopsodontids.

The relationships of *Diacodon* have been considered at length by Novacek (1982), who described for the first time much more complete material than was originally known for this genus. *Diacodon* has served as a taxon for as many as twelve species, but Novacek (1982) concluded that only the type species, *D. alticuspis,* is referable to this genus. Although *Diacodon* was traditionally regarded as a leptictid, this relationship is contradicted by features of the posterior premolars and molars that suggest affinities with erinaceomorphs. Nonetheless, this genus shows a more primitive overall morphology than other erinaceomorphs (with the possible exception of *Adunator*) and it is excluded from both the Dormaaliidae and the Erinaceidae.

Gingerich (1983), following Krishtalka (1976a), justifiably separated *Litolestes notissimus* (fig. 11) and *L. lacunatus* from the type species of that genus, *L. ignotus.* He established a new genus, *Litocherus,* to include *L. notissimus, L. lacunatus* and a new species, *L. zygeus. Litocherus* was designated by Gingerich as the type genus of the subfamily Litocherinae, to which he referred *Leipsanolestes, Litolestes, Mckennatherium,* and the new genera *Cedrocherus* and *Diacocherus.* We endorse Gingerich's (1983) recognition of *Litocherus,* although we note that his diagnoses distinguishing species of this genus were essentially limited to comparisons of size. Not mentioned were the more robust proportions of the protoconid and elongation of the talonid in P_4, and the reduced molar paraconids of *L. zygeus* that separate this species from *L. notissimus.*

Litocherus is another taxon potentially confused with hyopsodontid condylarths. Nevertheless, Gingerich (1983, p. 235) correctly noted that *Litocherus* is separable from *Haplaletes* and other primitive hyopsodontids by its sharper-cusped cheek teeth, the sweeping postmetacrista (lacking in upper molars of *Haplaletes*) and the lack of distinct labial cingula on the lower molars. Furthermore, at least unworn lower molars of *Litocherus* have a crestiform paraconid rather than the lophid, or shelflike paraconid characteristic of hyopsodontids.

Despite the validity of *Litocherus,* its status as the type genus for the Litocherinae *sensu* Gingerich (1983) is highly questionable. The subfamily was defined primarily on the lack of the specializations seen in "adapisoricines" (=*Adapisorex*) and "dormaaliines"—namely the presence of less reduced anterior

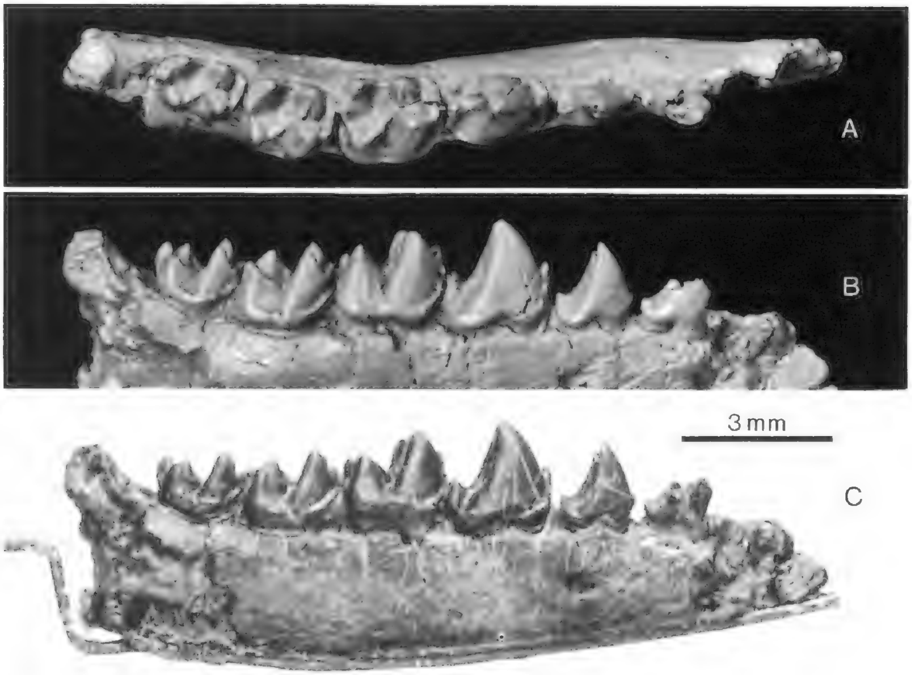

FIG. 11. *Litocherus notissimus,* right ramus with P_2 (damaged), P_{3-4}, M_{1-3} and alveoli for C, P_1 (AMNH 33938). A, occlusal; B, lateral views of epoxy cast; C, lateral view of original. Specimen from Scarrit Quarry, Fort Union Formation (upper Paleocene), Crazy Mountain Field, Montana.

premolars, more transverse upper molars, and smaller hypocones on upper molars. Some putative diagnostic characters do, as Gingerich maintained, distinguish "litocherines" from "adapisoricines" but these are shared with typical dormaaliids (e.g., metacone on P^4 small or absent). Other "diagnostic" characters allow great latitude in structural variation (e.g., P_4 talonid small, flat, *or* shallowly basined, lower molars with trigonids of moderate size, and basined talonids of moderately large size). Some traits do not really characterize all litocherines in a way that collectively distinguish them from certain other erinaceomorphs (e.g., "reduced" paraconids on lower molars).

Thus, the definition of Litocherinae does not successfully account for its included taxa nor does it effectively eliminate more plausible alternative relationships. *Leipsanolestes, Cedrocherus* and, particularly, *Litolestes* show erinaceid specializations that contrast strongly with the more general conditions in *Mckennatherium, Litocherus,* and *Diacocherus* (see also Gingerich, 1983, table 3). Moreover, *Diacocherus* (including "*Diacodon*" *minutus*) and *Mckennatherium* strongly differ from the more bunodont molar condition and swollen P_4 protoconids of *Litocherus.* We conclude that three "litocherines" (*Leipsanolestes, Litolestes,* and *Cedrocherus*) are better recognized as members of the Erinaceidae and that a special association between *Litocherus* and *Diacocherus* is unwarranted. *Litocherus* is a distinct taxon but its relationship with other erinaceomorphs is uncertain.

Gingerich's (1983, p. 238) recognition of *Diacocherus* illustrates the problem of untangling the "*Diacodon*" *minutus–Mckennatherium–Adunator* complex. Subtle differences in molar proportions distinguish *Diacocherus minutus* from *Mckennatherium* (Krishtalka, 1976a; Gingerich, 1983) but no characters

were specified to distinguish *Diacocherus minutus* and Gingerich's new species *Diacocherus meizon* from *Adunator lehmanni.* Perhaps *Adunator* best serves as the senior synonym of *Mckennatherium* and *Diacocherus.* Regardless of the nomenclatural solution, these species undoubtedly represent a close grouping of very small erinaceomorphs with sectorial, primitive dentitions.

Talpavus and *Talpavoides* show a basic similarity with dormaaliids. Yet these taxa—at least based on the meager available material—lack the important specializations that define the Dormaaliidae. In this regard they are somewhat "intermediate" in dental structure between the *Adunator–Diacocherus* complex and dormaaliids like *Scenopagus. Talpavus* and *Talpavoides,* for example, have an elongate P_4 with a well-developed talonid that is primitively uncharacteristic of dormaaliids. *Talpavus* also lacks the typical erinaceid specializations seen in progressive size decrease M_1 to M_3 and the salient paraconids on M_{1-2}. Although we have earlier included *Talpavus* and *Talpavoides* with the Dormaaliidae, it seems more realistic to regard these taxa as *incertae sedis,* until better material may show otherwise.

LITERATURE CITED

Bown, T. M.
1979. Geology and mammalian paleontology of the San Creek Facies, Lower Willwood Formation (lower Eocene) Washakie County, Wyoming. Wyoming Geol. Surv. Mem., vol. 2, pp. 1–151.

Bown, T. M., and D. Schankler
1982. A review of the Proteutheria and Insectivora of the Willwood Formation (lower Eocene) Bighorn Basin, Wyoming. U.S. Geol. Surv. Bull., no. 1523, pp. 1–79.

Butler, P. M.
1948. On the evolution of the skull and teeth in the Erinaceidae, with special reference to the material in the British Museum. Proc. Zool. Soc., London, vol. 118, pp. 446–500.
1956a. The skull of *Ictops* and the classification of the Insectivora. Proc. Zool. Soc., London, vol. 126, pp. 453–481.
1956b. Erinaceidae from the Miocene of East Africa. Fossil Mammals of Africa, vol. 11, pp. 1–75.
1972. The problem of insectivore classification. *In* Joysey, K. A., and T. S. Kemp (eds.), Studies in vertebrate evolution, pp. 253–265. New York, Winchester Press.

Clemens, W. A.
1973. Fossil mammals of the type Lance Formation, Wyoming. Part III. Eutheria and summary. Univ. Calif. Publ. Geol. Sci., vol. 94, pp. 1–102.

Cope, E. D.
1875. Systematic catalogue of the Vertebrata of the Eocene of New Mexico. Jour. Acad. Nat. Sci., Philadelphia, 1875, pp. 1–36.

Cuvier, G.
1817. La Regne Animal. Paris, Deterville, vol. 1, xxxvii + 504 pp.

Delson, E.
1971. Fossil mammals of the early Wasatchian Powder River local fauna, Eocene of northeast Wyoming. Bull. Amer. Mus. Nat. Hist., vol. 146, pp. 305–364.

Fischer de Waldheim, G. F.
1817. Adversia Zoologica. Part 2. De systemata mammalium. Mem. Soc. Imperiale Naturalistes, Mosquae, vol. 5, pp. 368–391.

Fox, R. C.
1983. New evidence on the relationships of the Tertiary insectivoran *Ankylodon* (Mammalia). Canadian Jour. Earth Sci., vol. 20, no. 6, pp. 968–977.

Galbreath, E. C.
1953. A contribution to the Tertiary geology and paleontology of northeastern Colorado. Univ. Kansas Paleo. Contr., vol. 4, pp. 1–119.

Gazin, C. L.
1959. Early Tertiary *Apheliscus* and *Phenacodaptes* as pantolestid insectivores. Smithsonian Miscel. Coll., no. 139, pp. 1–7.

Gingerich, P. D.
1983. New Adapisoricidae, Pentacodontidae, and Hyopsodontidae (Mammalia, Insectivora and Condylarthra) from the late Paleocene of Wyoming and Colorado. Contrib. Mus. Paleo., Univ. Michigan, vol. 26, no. 11, pp. 227–255.

Gregory, W. K.
1910. The orders of mammals. Bull. Amer. Mus. Nat. Hist., vol. 27, pp. 1–524.

Heller, F.
1935. *Amphilemur eocaenicus* n. g. et n. sp.,

ein primitiver Primate aus dem Mitteleozän des Geiseltales bei Halle a. S. Nova Acta Leopoldina, N.F., vol. 2, no. 3, pp. 293–300.

Hürzeler, J.
1946. *Gesneropithex peyeri* nov. gen. nov. spec., ein neuer Primate aus dem Ludien von Gösgen (Solothurn). Ecl. Geol. Helv., vol. 39, pp. 354–361.
1947. *Alsaticopithecus leemanni* nov. gen. nov. spec., ein neuer Primate aus dem unteren Lutetien von Buchsweiler im Unterelsass. Ecl. Geol. Helv., vol. 40, pp. 343–356.

International Code of Zoological Nomenclature
1964. Adopted by the XV International Congress of Zoology (Stoll et al., eds.). International Trust for Zoological Nomenclature, London.

Jepsen, G. L.
1930. Stratigraphy and paleontology of the Paleocene of northeastern Park County, Wyoming. Proc. Amer. Phil. Soc., vol. 69, pp. 463–528.

Koenigswald, W. von, and G. Storch
1983. *Pholidocercus hassiacus,* ein Amphilemuride aus dem Eozän der "Grube Messel" bei Darmstadt (Mammalia, Lipotyphla). Senckenbergiana Lethaea, vol. 64, pp. 447–495.

Krishtalka, L.
1976a. Early Tertiary Adapisoricidae and Erinaceidae (Mammalia: Insectivora) of North America. Bull. Carnegie Mus. Nat. Hist., vol. 1, pp. 1–40.
1976b. North American Nyctitheriidae (Mammalia: Insectivora). Ann. Carnegie Mus. Nat. Hist., vol. 46, pp. 7–28.
1977. Early Eocene Euramerican Insectivora. GeoBios, Mem. Spec., vol. 1, pp. 135–139.

Krishtalka, L., and T. Setoguchi
1977. Paleontology and geology of the Badwater Creek area, central Wyoming. Part 13. The late Eocene Insectivora and Dermoptera. Ann. Carnegie Mus. Nat. Hist., vol. 46, pp. 71–99.

Krishtalka, L., and R. M. West
1977. The paleontology and geology of the Bridger Formation southern Green River Basin, southwestern Wyoming. Part 2. The Bridgerian insectivore *Entomolestes grangeri.* Contr. Biol. Geol., Milwaukee Publ. Mus., vol. 14, pp. 1–11.

Lemoine, V.
1883. Etude sur le *Neoplagiaulax* de la faune éocène inférieure des environs de Reims. Bull. Soc. Géol. France, 3rd ser., vol. 11, pp. 249–271.

Lillegraven, J. A., M. C. McKenna, and L. Krishtalka
1981. Evolutionary relationships of middle Eocene and younger species of *Centetodon* (Mammalia, Insectivora, Geolabididae) with a description of the dentition of *Ankylodon* (Adapisoricidae). Univ. Wyoming Publ., vol. 45, pp. 1–115.

Linnaeus, C.
1758. Systema Naturae per Regna Tri Naturae. Editio decima, reformata. Stockholm, Laurentii Salvii, 824 pp.

McDowell, S. B.
1958. The Greater Antillean insectivores. Bull. Amer. Mus. Nat. Hist., vol. 115, pp. 113–124.

McGrew, P.
1959. Geology and paleontology of the Elk Mountain and Tabernacle Butte area, Wyoming. Bull. Amer. Mus. Nat. Hist., vol. 117, pp. 121–176.

McKenna, M. C.
1960. Fossil Mammalia of the early Wasatchian Four Mile fauna, Eocene of northwest Colorado. Univ. Calif. Publ. Geol. Sci., vol. 37, pp. 1–130.
1975. Toward a phylogenetic classification of the Mammalia. *In* Luckett, W. P., and F. S. Szalay (eds.), Phylogeny of the primates: a multidisciplinary approach, pp. 21–46. New York, London, Plenum Press.

McKenna, M. C., P. Robinson, and D. W. Taylor
1962. Notes on Eocene Mammalia and Mollusca from Tabernacle Butte, Wyoming. Amer. Mus. Novitates, no. 2102, pp. 1–33.

McKenna, M. C., and G. G. Simpson
1959. A new insectivore from the middle Eocene of Tabernacle Butte, Wyoming. Amer. Mus. Novitates, no. 1952, pp. 1–12.

Maier, W.
1979. *Macrocranion tupaiodon,* an adapisoricid (?) insectivore from the Eocene of the "Grube Messel" (Western Germany). Paläont. Zeitschr., vol. 53, pp. 38–62.

Marsh, O. C.
1872. Preliminary description of new Tertiary mammals. Amer. Jour. Sci., vol. 4, pp. 122–128, 202–224.

Matthew, W. D.
1909. The Carnivora and Insectivora of the

Bridger Basin. Mem. Amer. Mus. Nat. Hist., vol. 9, pp. 289–567.
1918. A revision of the lower Eocene Wasatch and Wind River Faunas. *In* Article XVI (by W. D. Matthew and W. Granger); Part V. Insectivora (cont'd.), Glires, Edentata. Bull. Amer. Mus. Nat. Hist., vol. 38, pp. 565–657.

Novacek, M. J.
1973. Insectivora of the late Eocene (Uintan) of San Diego County, California. Master's Thesis, San Diego State Univ., 301 pp.
1976. Insectivora and Proteutheria of the later Eocene (Uintan) of San Diego County, California. Contr. Sci., L.A. County Nat. Hist. Mus., no. 283, pp. 1–52.
1977. A review of Paleocene and Eocene Leptictidae (Eutheria: Mammalia) from North America. PaleoBios, vol. 24, pp. 1–42.
1980. *Crypholestes,* a new name for the Early Tertiary insectivore (Mammalia) *Cryptolestes* Novacek 1976. Jour. Paleo., vol. 54, p. 1135.
1982. *Diacodon alticuspis,* an erinaceomorph insectivore from the early Eocene of northern New Mexico. Univ. Wyoming, Contrib. Geol. 20, vol. 2, pp. 135–149.

Patterson, B., and P. O. McGrew
1937. A soricid and two erinaceids from the White River Oligocene. Field Mus. Nat. Hist., Geol. Ser., vol. 6, pp. 245–272.

Quinet, G. E.
1964. Morphologie dentaire des mammifères éocène de Dormaal. Bull. Groupement Internatl. Rech. Sci. Stomatologie, vol. 7, pp. 272–294.

Rich, T. H.
1981. Origin and history of the Erinaceinae and Brachyericinae (Mammalia, Insectivora) in North America. Bull. Amer. Mus. Nat. Hist., vol. 171, pp. 1–116.

Rich, T. H., and P. V. Rich
1971. *Brachyerix,* a Miocene hedgehog from western North America, with a description of the tympanic regions of *Paraechinus* and *Podogymnura.* Amer. Mus. Novitates, no. 2477, pp. 1–58.

Russell, D. E.
1964. Les mammifères Paléocène d'Europe. Mém. Mus. Natl. Hist. Nat., ser. C, vol. 13, pp. 1–324.

Russell, D. E., P. Louis, and D. E. Savage
1975. Les Adapisoricidae de l'Éocène inférieur de France: reévaluation des formes considérées affines. Bull. Mus. Natl. Hist. Nat., vol. 327, pp. 129–193.

Saban, R.
1954. Phylogenie des insectivores. Bull. Mus. Natl. Hist. Nat., ser. 2, vol. 26, pp. 419–432.

Schankler, D. M.
1980. Faunal zonation of the Willwood Formation in the central Bighorn Basin, Wyoming. *In* Gingerich, P. D. (ed.), Early Cenozoic paleontology and stratigraphy of the Bighorn Basin, Wyoming, pp. 99–118. Univ. Michigan, Papers in Paleo., no. 24.

Schlosser, M.
1887. Die Affen, Lemuren, Chiropteren, Insectivora, Marsupialier, Creodonten und Carnivoren des europäischen Tertiärs. Teil 1. Beiträge zur Paläontologie Oesterreich-Ungarns.

Schmidt-Kittler, N.
1973. *Dimyloides*—Neufunde aus der ober-Oligozänen Spaltenfüllung "Ehrenstein 4" (Süddeutschland) und die systematische Stellung der Dimyliden (Insectivora, Mammalia). Mitt. Bayer. Staatsam. Paläont. u. hist. Geol., vol. 13, pp. 115–139.

Sigé, B.
1977. Insectivores primitifs de l'Éocène supérieur et Oligocene inférieur d'Europe occidentale. Nyctitheriides. Mém. Mus. Natl. Hist. Nat., ser. C, vol. 4, pp. 1–140.

Simpson, G. G.
1928. A new mammalian fauna from the Fort Union of southern Montana. Amer. Mus. Novitates, no. 297, pp. 1–15.
1935. New Paleocene mammals from the Fort Union of Montana. Proc. U.S. Natl. Mus., vol. 83, pp. 221–244.
1945. The principles of classification and a classification of the mammals. Bull. Amer. Mus. Nat. Hist., vol. 85, pp. 1–350.

Stock, C.
1935. Insectivora from the Sespe Uppermost Eocene, California. Proc. Natl. Acad. Sci., vol. 20, pp. 349–354.

Teilhard de Chardin, P.
1927. Les mammifères de l'Éocène inférieur de la Belgique. Mém. Mus. Hist. Nat. Belgique, vol. 36, pp. 1–33.

Tobien, H.
1962. Insectivoran (Mamm.) aus dem Mitteleozän (Lutetium) von Messel bei

Darmstadt. Notizbl. Hessischen Landesamt Bodenforsch., vol. 90, pp. 7–47.

Van Valen, L.

1965. A middle Paleocene primate. Nature, vol. 207, no. 4995, pp. 435–436.

1967. New Paleocene insectivores and insectivore classification. Bull. Amer. Mus. Nat. Hist., vol. 132, pp. 1–126.

Weitzel, K.

1949. Neue Wirbeltiere (Rodentia, Insectivora, Testudinata) aus dem Mitteleozän von Messel bei Darmstadt. Abhandl. Senckenberg Naturforsch. Gesellsch., no. 480, pp. 1–24.

Zdansky, O.

1930. Die alttertiären Säugetiere Chinas nebst stratigraphischen Bemerkungen. Palaeont. Sinica, ser. C, vol. 6, no. 2, pp. 1–87.